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THE CROCODILIAN GENUS PALEOSUCHUS

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Extensive field work in the Intendencia Meta and the Comisaría Vaupés and Amazonas, Colombia, over a period of six years has enabled me to observe both species of the little known crocodilian genus *Paleosuchus*. This genus differs from the closely related *Caiman* in various characteristics but most obviously in the completely ossified palpebrals (bony eyelids) and the lack of the transverse preorbital ridge. The latter characteristic has given the two species the name "smooth fronted caimans." They are to be found mainly in the Amazon and Orinoco basins (Schmidt, 1928), where they live in the general area with *Caiman sclerops* and *Melanosuchus niger* but occur in a restricted ecological niche.

The opportunity to study the material in the United States was generously granted by the John Simon Guggenheim Memorial Foundation, to which I express my sincerest gratitude. Further, I wish to express my appreciation of much valuable advice and helpful criticism from the late Dr. Karl P. Schmidt. I also want to thank Dr. Rainer Zangerl, Curator of Fossil Reptiles, for his kind co-operation in preparing x-ray photographs for special studies, and Mr. Clifford H. Pope, Dr. Robert F. Inger, and Mr. Hymen Marx, of the Division of Reptiles, for much aid. I am also indebted to Mr. Arthur Loveridge, of the Museum of Comparative Zoology (MCZ); Mr. Charles M. Bogert and Mrs. Bessie M. Hecht, of the American Museum of Natural History (AMNH); and Dr. Robert C. Stebbins, of the Museum of Vertebrate Zoology, Berkeley, University of California (MVZ), for the loan of material and facilities kindly given for studies on the specimens in their collections. The skull drawings were done by Miss Phyllis Wade, Department of Zoology, Chicago Natural History Museum, whom I wish to thank. Acknowledgment is also due to Dr. John Hendrickson, University of Malaya, and to Mr. Robert Snedigar, Brookfield Zoo, Brookfield, Illinois, for their

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valuable information on ecology. Highly appreciated is the support of Dr. Julian de Zulueta, former chief of research of the Instituto "Roberto Franco" in Villavicencio, and that of Dr. Richard E. Schultes, Curator, Botanical Museum, Harvard University, whose companionship I enjoyed on several expeditions. My thanks also go to Dr. Miguel Dumit, Director of the Empresa Cauchera A.I.D.A., Bogotá, for many facilities. The success in collecting the Colombian material is largely the result of the great ability and indefatigable work of my companions and hunters, the Señores Isidoro Cabrera, Carlos A. Velásquez and Carlos Balcázar.

NOMENCLATURE

The genus *Paleosuchus*, although well established, has not been adequately defined even in some recent literature. The general synonymy, avoiding mere reiterations, is as follows:

Paleosuchus Gray

Paleosuchus Gray, 1862, Ann. Mag. Nat. Hist., (3), **10**: 330—type of *Crocodilus trigonatus* Schneider (proposed as subgenus of *Caiman*).

Crocodylus Laurenti, 1768, Syn. Rept., p. 53 (part).

Alligator Cuvier, 1807, Ann. Mus. Hist. Nat. Paris, **10**: 25 (part); Strauch, 1866, Mém. Acad. Sci. St. Petersb., (7), **10**, no. 13, p. 9 (part).

Jacaretinga Spix, 1825, Animalia nova . . . lacertarum . . ., p. 1 (part); Mook and Mook, 1940, Amer. Mus. Nov., no. 1098, p. 7; Dunn, 1945, Caldasia, **3**: 333; Carvalho, 1951, Arq. Mus. Nac., **42**: 129.

Champsa Wagler, 1830, Syst. Amphib., p. 140 (part).

Caiman (subgenus, not of Spix) Duméril and Bibron, 1836, Erp. Gén., **3**: 63; Gray, 1844, Cat. Tortoises, Crocodiles . . ., p. 66 (part); Duméril and Duméril, 1851, Cat. Méth., p. 26 (part); Boulenger, 1889, Cat. Chel. . . . Brit. Mus., p. 291 (part); Mook, 1921, Bull. Amer. Mus. Nat. Hist., **44**: 244.

Aromosuchus Gray, 1862, Ann. Mag. Nat. Hist., (3), **10**: 330—type of *Crocodilus palpebrosus* Cuvier (proposed as a subgenus of *Caiman*).

Crocodylus (not of Laurenti) Müller, 1924, Zool. Anz., **58**: 316; Werner, 1933, Tierreich, Liefg. 62, p. 34.

The synonymy of *Paleosuchus* is peculiarly complicated by the varying use of *Jacaretinga* Spix, which included *moschifer* (=*trigonatus*), a species of *Paleosuchus*, with *punctulatus* (=*sclerops*), a species of spectacled caiman. The transfer of Spix's name *Caiman* from the spectacled caimans to *Paleosuchus* by Gray has occasionally been followed. Müller's still more radical proposal to restrict the name *Crocodylus* to the smooth-fronted caimans produces so much nomenclatural confusion that it should under no circumstances be followed.

The type of *Jacaretinga* is fixed by Müller as *punctulatus*, and the long use of *Caiman* for the spectacled caimans makes it desirable to place *Jacaretinga* definitively in the synonymy of *Caiman*.

Paleosuchus palpebrosus Cuvier

Crocodilus palpebrosus, var. 1, Cuvier, 1807, Ann. Mus. Hist. Nat. Paris, **10**: 28, pl. 1, figs. 6, 17, pl. 2, fig. 2—Cayenne.[1]

Crocodilus (*Alligator*) *palpebrosus* Merrem, 1820, Tent. Syst. Amphib., p. 34.

Alligator palpebrosus Duméril and Bibron, 1836, Erp. Gén., **3**: 67 (var. A); Strauch, 1866, Mém. Acad. Sci. St. Petersb., (7), **10**, no. 13, p. 25.

Jacaretinga palpebrosus Vaillant, 1898, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **10**: 171; Mook and Mook, 1940, Amer. Mus. Nov., no. 1098, p. 7; Dunn, 1945, Caldasia, **3**: 333.

Champsa palpebrosa Wagler, 1830, Syst. Amphib., p. 140; Natterer, 1841, Ann. Wien. Mus., **2**: 324, pl. 27.

Caiman palpebrosus Gray, 1844, Cat. Tortoises, Crocodiles . . ., p. 67; Boulenger, 1889, Cat. Chel. . . . Brit. Mus., p. 296.

Caiman (*Aromosuchus*) *palpebrosus* Gray, 1862, Ann. Mag. Nat. Hist., (3), **10**: 330.

Paleosuchus palpebrosus Müller, 1924, Zeitschr. Morph. Ökol. Tiere, **2**: 441, pl. 5, fig. 31; Schmidt, 1928, Field Mus. Nat. Hist., Zool. Ser., **12**: 210, fig. 1; Mertens, 1943, Senckenbergiana, **26**: 280, pl. 4; Wermuth, 1953, Mitt. Zool. Mus. Berlin, **29**: 455, figs. 33, 34.

Crocodylus palpebrosus Werner, 1933, Tierreich, Liefg. 62, p. 35, fig. 33.

Champsa gibbiceps Natterer, 1841, Ann. Wien. Mus., **2**: 324, pl. 28—Ribeirão do Guacurizal, a mountain brook near Jacobina, 3 miles east of Villa Maria, Rio Paraguay, Mato Grosso.

Paleosuchus trigonatus Schneider

Crocodylus niloticus Laurenti, 1768, Syn. Rept., p. 53 (part).

Crocodilus trigonatus Schneider, 1801, Hist. Amphib., p. 161, pls. 1, 2 — no locality.

Alligator trigonatus Merrem, 1820, Tent. Syst. Amphib., p. 34; Strauch, 1866, Mém. Acad. Sci. St. Petersb., (7), **10**, no. 13, p. 27.

Caiman trigonatus Gray, 1844, Cat. Tortoises, Crocodiles . . ., p. 66; Boulenger, 1889, Cat. Chel. . . . Brit. Mus., p. 296.

Jacaretinga trigonatus Vaillant, 1898, Nouv. Arch. Mus. Hist. Nat. Paris, (3), **10**: 174, 177, 180, fig. 1; Mook and Mook, 1940, Amer. Mus. Nov., no. 1098, p. 7; Dunn, 1945, Caldasia, **3**: 333.

Champsa trigonata Wagler, 1830, Syst. Amphib., p. 140; Natterer, 1841, Ann. Wien. Mus., **2**: 323, pl. 26.

[1] Vaillant (1898, pl. 174) has shown that the type specimen of Cuvier's *palpebrosus*, var. 1, is also the type of *Alligator palpebrosus*, var. A, of Duméril and Bibron (Mus. Hist. Nat. Paris no. 7530).

Paleosuchus trigonatus Schmidt, 1928, Field Mus. Nat. Hist., Zool. Ser., **12**: 209, fig. 1; Mertens, 1943, Senckenbergiana, **26**: 278, pl. 3; Wermuth, 1953, Mitt. Zool. Mus. Berlin, **29**: 452, figs. 31, 32.

Crocodilus palpebrosus, var. 2, Cuvier, 1807, Ann. Mus. Hist. Nat. Paris, **10**: 38, pl. 2, fig. 1.[1]

Alligator palpebrosus, var. B, Duméril and Bibron, 1836, Erp. Gén., **3**: 72.

Jacaretinga moschifer Spix, 1825, Animalia nova . . . lacertarum . . ., p. 1, pl. 1—Bahia.

Crocodylus niloticus Müller, 1924, Zool. Anz., **58**: 319; Werner, 1933, Tierreich, Liefg. 62, p. 35.

Jacaretinga moschifer, as pointed out by Vaillant, is a composite of *trigonatus* and *palpebrosus*. In my opinion it is best placed in the synonymy of *trigonatus*, especially in view of the *trigonatus* pattern of the lower jaw in Spix's figure, and the configuration of the snout.

SPECIMENS EXAMINED

Paleosuchus palpebrosus.—COLOMBIA: Intendencia Meta: Sabana de San Juan de Arama, Caño Choriaro (CNHM 2; MVZ 4); Caño El Mico (CNHM 1; MVZ 1); upper Río Cunimia (CNHM 1); Caño Manacales (CNHM 1); Serrania de la Macarena, Caño Guapaya (Medem collection 1); Villavicencio, Caño Cajuy (CNHM 2; Medem collection 3); Caño Aguas Claras (Medem collection 2); Río Ocoa (Medem collection 1). Comisaría Amazonas: Río Apaporis (CNHM 2; Medem collection 1); Caño Churucu (Senckenberg Mus. 1); Caño Inaná (CNHM 2). Comisaría Vaupés: upper Río Guaviare (Medem collection 2).

BRAZIL: Ubinga, Para (CNHM 1); Cucuhy (AMNH 1).

BRITISH GUIANA: (AMNH 1).

ECUADOR: Río Bobonaza, Anga Cocha (AMNH 1).

PERU: Río Pastaza, Andoas (AMNH 4).

Paleosuchus trigonatus.—COLOMBIA: Intendencia Meta: Río Cafre (CNHM 1; Medem collection 10); Río Ocoa, 5 km. south of Villavicencio (CNHM 1); Serrania de la Macarena, Río Sansa (Medem collection 1). Comisaría Amazonas: lower Río Caquetá, Puerto Córdoba (CNHM 1); Leticia (Medem collection 1); upper Río Apaporis (CNHM 4; Medem collection 1); Caño Churucu (CNHM 1); Río Pacoa (CNHM 5; Senckenberg Mus. 1); upper Caño Tacunemita (Medem collection 3); Yay-Gojé, lower Río Apaporis (New York

[1] Vaillant (loc. cit.) shows that the type of Cuvier's *palpebrosus*, var. 2, is a specimen of *trigonatus* (Mus. Hist. Nat. Paris no. 7525); the type of Duméril and Bibron's *palpebrosus*, var. B, is no. 7527.

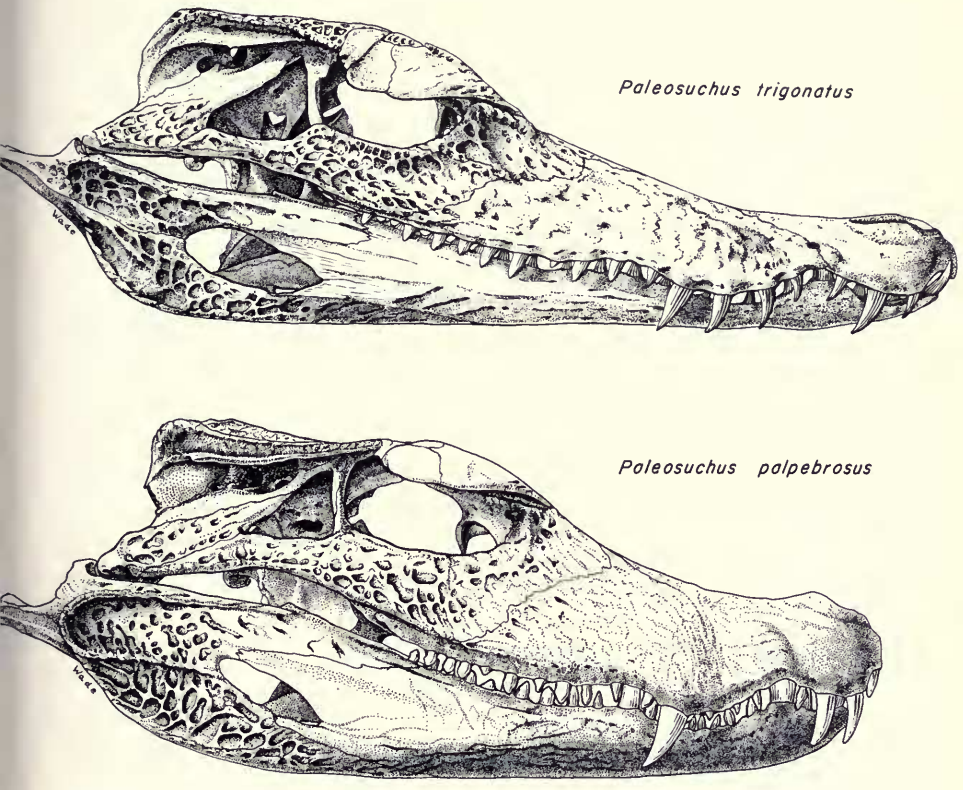

FIG. 35. Lateral view of skulls of *Paleosuchus trigonatus* and *P. palpebrosus*.

Zoological Society 2). Comisaría Vaupés: Caño Grande, tributary of Río Inirida (Medem collection 1); Caño Cuduyari, tributary of Río Vaupés (Medem collection 1); upper Río Vaupés (Medem collection 1).

BRAZIL: Para (MCZ 1); Vigia near Obydos (MCZ 1); upper Amazonas (AMNH 1); Brazil(?) (AMNH 2).

BRITISH GUIANA: Kartabo (AMNH 4); upper Essequibo River (AMNH 3).

PERU: Río Ucayali, Iquitos (AMNH 1).

SKULL CHARACTERS

Very few skulls of *Paleosuchus palpebrosus* and *P. trigonatus* have hitherto been available for study. The first recognizable figure of the skull of a species of *Paleosuchus* appears to be that of *trigonatus*

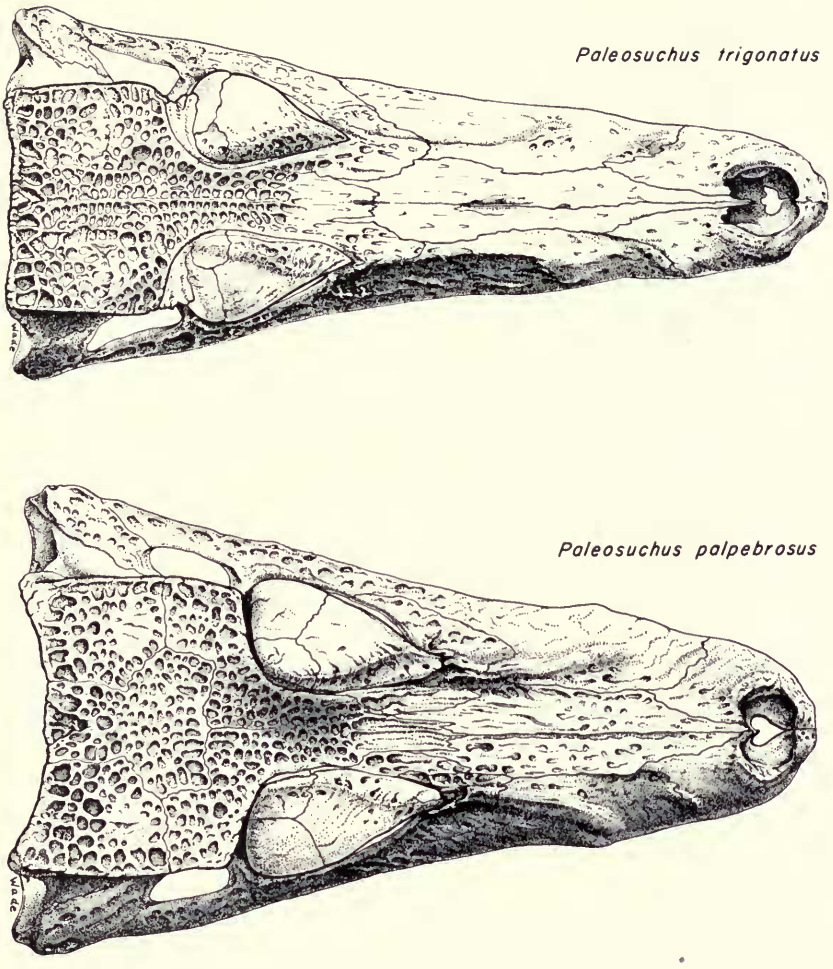

FIG. 36. Dorsal view of skulls of *Paleosuchus trigonatus* and *P. palpebrosus*.

in Schneider (1801, pls. 1, 2), which is without legend, although he is the describer of this species. Cuvier (1807, pl. 1, figs. 6, 17) presented the first figure of a skull of *palpebrosus;* he also gave a figure and description of the occipital sectors of his *Crocodilus palpebrosus* var. 1 and 2 (op. cit., pl. 2, figs. 1, 2). D'Alton and Burmeister (1854, pl. 1, fig. 1, pl. 3, fig. 3) gave a short account of another skull designated as *palpebrosus,* but this is obviously a *trigonatus,* as shown by a number of features. Brühl (1862, pl. 19) copied the orbital region of the same skull to demonstrate the palpebrals.

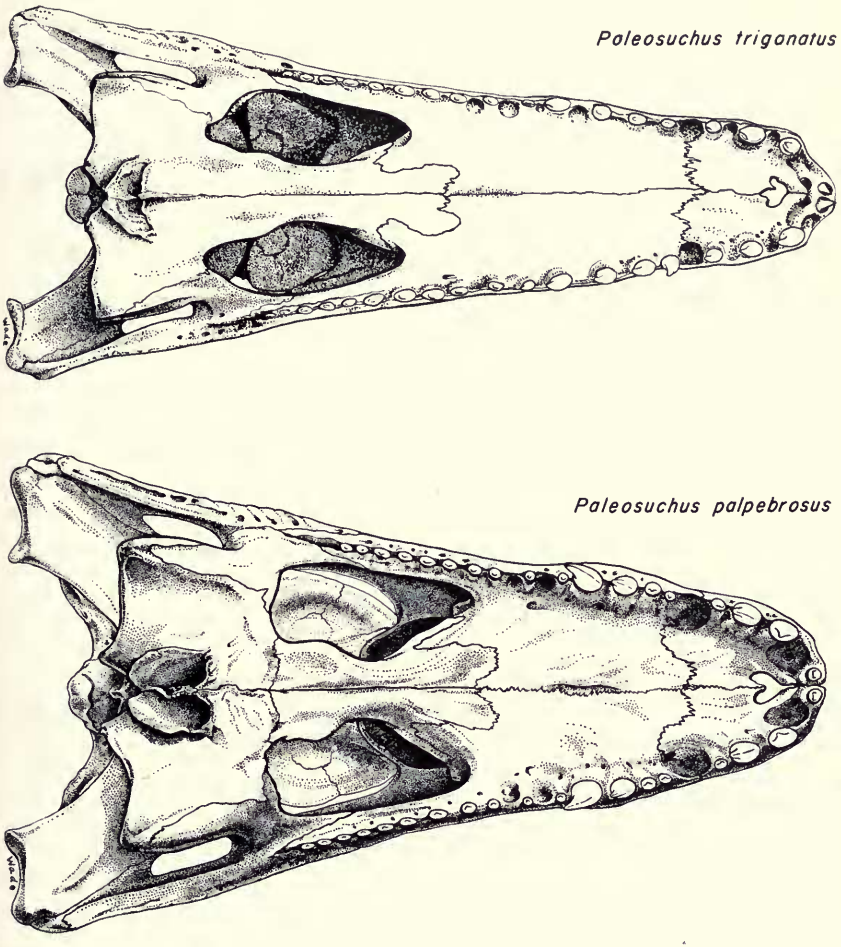

FIG. 37. Ventral view of skulls of *Paleosuchus trigonatus* and *P. palpebrosus*.

More adequate descriptions have appeared in recent time. Mook (1921) describes the skull of a single juvenile specimen of *trigonatus*. Kälin (1933) deals with both species (three skulls of *palpebrosus;* three juvenile *trigonatus*). Mertens (1943) indicates several important cranial differences between the two species, based on skulls of one adult and two juvenile *palpebrosus* and those of two adults of *trigonatus*. In spite of these detailed descriptions there are several discrepancies between the accounts of these authors, primarily because most of their specimens were juveniles. The differences between juvenile and adult skulls, so common in crocodilians, are

especially marked in the genus *Paleosuchus* on account of the strong ossification during growth. In addition to the variations resulting from age, individual differences within each species are discernible. My own observations are based on the following numbers of skulls: *palpebrosus*, 8 adults, 5 subadults, and 2 juveniles; *trigonatus*, 9 adults, 2 subadults, and 12 juveniles. The size ranges of these skulls are: *palpebrosus* 92–194 mm., *trigonatus* 101–324 mm.

The skull of *palpebrosus* is conspicuously broader, shorter, and deeper than that of *trigonatus* (figs. 35–37). The snout of the former is compressed and has a broad, upturned tip, whereas that of *trigonatus* is elongate and narrow. The "dog-like" shape of the *palpebrosus* skull is expressed in a trend toward shorter and broader individual bones. Medially, the slope of the preorbital region is much steeper in *palpebrosus*. A prominent canthus rostralis runs between the lacrimal and fourth maxillary tooth in *palpebrosus*, giving the maxilla a very steep lateral slope. Though its lacrimal is elevated, *trigonatus* has no canthus rostralis, with the result that the maxilla is rounded laterally.

The maximum length of the nasal aperture is relatively longer in *trigonatus*, as is the projection of the nasals into the aperture. In *palpebrosus* the nasals usually fuse in adults, but in *trigonatus* they always retain the median suture, which develops into a characteristic longitudinal groove in adults.

Supratemporal fossae are not evident even in juvenile *palpebrosus*. In *trigonatus* these fossae are distinctly evident in juveniles and subadults (skulls to 14.6 cm.), and even in adults (skulls to 21.7 cm.) half-moon-shaped sutures are discernible. Kälin (1933) is under the mistaken impression that the fossae are obliterated at an early age in *trigonatus*.

The external mandibular foramen is larger in *trigonatus* than in *palpebrosus*. Its edges are always smooth in the former, jagged in the latter. The palatal fenestrae also differ sharply. In *palpebrosus* they are nearly kidney-shaped and very wide at the posterior end. Those of *trigonatus* are narrower, especially posteriorly.

In general, the skull of *trigonatus* is more deeply sculptured. This difference is particularly noticeable on the lacrimal and jugal (figs. 35–37).

Many of the differences between the skulls of *palpebrosus* and *trigonatus* result from their different degrees of ossification, which is greater in *palpebrosus*. In the latter, one clearly observes the more pronounced tendency toward obliteration of all vacuities. Not only

are the vacuities larger in *trigonatus*, but some, for example the supratemporal fossae, are not present in *palpebrosus* at all. Although fusion of sutures is conspicuous in both species, this trend is carried farther in *palpebrosus;* the fate of the nasal suture illustrates this point. The shallower sculpturing of the skull of *palpebrosus* may also be viewed as resulting from greater ossification.

As pointed out by earlier authorities, the less specialized of the two species is *trigonatus*. Kälin (1933) refers to this species as more primitive, because of the non-closure of the supratemporal fossae in juveniles. Mertens (1943) refers to it as more "old-fashioned" (*altertümlicher*) because of the larger external mandibular foramen and the supratemporal fossae. *Paleosuchus trigonatus* is far more generalized, not only in its craniology but also in some external characters. Certain juvenile cranial features of *palpebrosus*, such as the narrower snout and the more pointed anterior projection of nasals, may be thought of as vestigial *trigonatus* characters in so far as they are specific for *trigonatus* and only present in juveniles of *palpebrosus* and not in all specimens of these.

Several authors have remarked on the parallelism between the West African *Osteolaemus*, a short-snouted and apparently primitive crocodile, and the genus *Paleosuchus*, perhaps the most primitive type of the family Alligatoridae. This parallelism extends to such details as the bony eyelid and the brown eye color, which must be independently derived. This matter is discussed by Kälin (1933) and Mertens (1943).

EXTERNAL CHARACTERS

Coloration.—As the coloration in life of both species has been described previously (Medem, 1952, 1953), it is sufficient here to note the principal differences between adults of the species. The cranial table of *palpebrosus* is bright reddish brown, that of *trigonatus* dark brown. The reddish lower jaw of the former usually bears four or five dark brown marks; although the lower jaw of *trigonatus* also bears alternate light and dark bands, the dark areas are the same color as the rest of the head while the light areas are yellow. Dorsally, the body and tail are very dark brown or blackish in *palpebrosus*, dark brown in *trigonatus*. Ventrally, the body and tail of *palpebrosus* are shiny black with large areas of light gray or horn brown in the center; *trigonatus* has just the opposite proportions, the light tones dominating and the dark tones restricted.

Juveniles of both species are brighter in coloration and have more distinctive markings than adults. Nevertheless, the specific charac-

teristics are evident; for example, the cranial table of young *palpebrosus* is bright yellowish and that of young *trigonatus* brown.

Dermal armor.—Both species have highly developed dermal bony plates dorsally and ventrally. The armor seems to be stronger in *palpebrosus*. Thus, the trend in this species to greater ossification, already seen in the skull, extends to the body.

Scutellation.—Since the time of Cuvier the arrangement of the occipitals has been thought to distinguish the two species; *palpebrosus* was said to have two rows and *trigonatus* one. Actually, of 37 *trigonatus* examined 28 have two rows of occipitals, independently of age or locality; *palpebrosus* almost invariably has two rows.

A statistical difference is evident in the number of cervicals. Fifteen *palpebrosus* have five transverse rows, eight have four rows, and four have three; twenty-one *trigonatus* have four rows, fifteen have five, and one has three.

Slight but distinct specific differences involve dorsals and ventrals. Every dorsal in *palpebrosus* has a keel extending its entire length. In *trigonatus* the outermost dorsals have short, triangular keels and the two innermost rows have vestigial keels or none. The broadest transverse row of dorsals usually has eight scales in *palpebrosus*, six in *trigonatus*. Similarly, the broadest transverse row of ventrals usually contains sixteen scales in *palpebrosus*, twelve in *trigonatus*. The former has from twenty-one to twenty-four transverse rows of ventrals and the latter from nineteen to twenty-four rows.

The lumbar scutes are arranged in three transverse rows in both species. Each row contains four scales in *palpebrosus*, except for two juveniles (24.0–24.7 cm., total length) each of which has two lumbar rows with a reduced number. Nine *trigonatus* have four scales in each lumbar row. In the fifteen others (distributed over the geographic and age ranges), one or two rows have fewer scales, the lowest number being two.

The double-crested base of the tail normally has ten segments (20 of 25 specimens) in *palpebrosus*, and nine (12 of 22) in *trigonatus*. The single-crested section of *palpebrosus* has from 17 to 21 segments, that of *trigonatus* from 17 to 19.

As in the cranial features, the dermal armor of *palpebrosus* is more specialized, with more constant characters, as in the occipital and lumbar scutes, and with a tendency to a larger number of transverse scale rows and a larger number of scales in both dorsal and ventral rows. Those on the base of the tail are slightly fewer. The shape of the keels is distinctive in each species, as is the scale arrange-

ment of the tail. The somewhat fewer scale rows and individual scales in both the dorsal and ventral armor of *trigonatus* are matched only by juvenile *palpebrosus*.

ECOLOGY

The only information available concerning the ecology of the two species of *Paleosuchus* consists of isolated notes. With justification, Schmidt (1928) states: "Their ecologic relations with the spectacled caimans offer one of the most interesting field problems in South American zoology."

Natterer (1841), who gave the first correct locality of *Paleosuchus trigonatus*, states that both species usually are found in the brooks of the tropical rain forest, but that sometimes they live in bayous, concealing themselves by day in burrows below the water level. He reports the capture of a specimen of *palpebrosus* in a burrow 1.5 meters deep in a dried-out swamp. Natterer also collected *palpebrosus* from the Paraguay drainage, in the Riberão da Guacurizal, a "mountain brook" near Jacobina, three miles east of Villa Maria. Natterer's term *"Gebirgsbach"* does not mean a brook within the mountains, but apparently one that originates in the mountains. *P. palpebrosus* has been collected in the same habitat in the Colombian Llanos Orientales. Müller (1912) observed that both species of *Paleosuchus* from the Island of Mexiana live in burrows situated beside brooks, or even in the woods. Mertens (1943) also refers to these caimans as predominantly inhabiting the brooks in tropical rain forests. My more extensive observations are still far from complete and should be considered as the basis for further and more extended investigation.

Ecological niche.—Paleosuchus palpebrosus and *P. trigonatus* are both found in a well-defined ecological niche (Medem, 1952, 1953). In general terms this is swift running water in the tropical rain forest (fig. 38). Both species of *Paleosuchus* and *Caiman sclerops* live in the upper Apaporis and its tributaries (Río Pacoa, Río Cananarí, Caño Churúcu, etc.), but in conspicuously different habitats. In small brooks (Caños, Igarapés) only the *Paleosuchus* are to be found. In smaller rivers, like the Pacoa, the *Paleosuchus* are always to be observed near small rapids or waterfalls and in the vicinity of the whirlpools. Such rapids are quite abundant, because the rivers break through the rocky areas produced by several isolated mountain ridges. The spectacled caimans are never to be found in this swift-water niche, but they are abundant in areas where the waters are more quiet, as in the large curves of the rivers (*vueltas*). In the

Apaporis itself *Paleosuchus* can be found with certainty near the mouths of smaller brooks, even the smallest, that flow into the river, and beside each whirlpool.

In the lagunas, mostly connected among themselves and with the river, I never observed any *Paleosuchus;* these waters apparently form the preferred ecological niche of *Caiman sclerops.* A fair illustration of the two different habitats is afforded by the laguna Inaná, connected with the Apaporis and consisting of three individual lagoons communicating with each other by a channel between nos. 1 and 2 and by a brook between nos. 2 and 3. The brook, about 500 meters long, runs through forest and has a swift current in which the water is lower in temperature than that of the lagoons. *Caiman sclerops* occurs in abundance in the lagoons, and only *Paleosuchus palpebrosus* is to be found in the brook itself and in laguna no. 2 near the mouth of the brook (Medem, 1953).

In the Llanos Orientales *Paleosuchus palpebrosus* and *trigonatus* have been collected mainly from small brooks in the forest islands; they were not observed in the lagunas situated in the open plains. These brooks and rivers have a swift current over a bed of large stones or gravel in their upper portions, that is, up to a distance of approximately 40 km. from the Cordillera Oriental.

It is evident that both species of *Paleosuchus* are limited to a particular ecological niche, although it can not be stated that they are absolutely bound to it and that they never go into lagunas or other quiet waters. *Caiman sclerops* (and probably other species) apparently avoid swift waters, though they are obviously able to enter such an environment temporarily.

Behavior and habits.—Observations on habits and behavior were made during several months of night hunting, and on three animals kept in captivity in their natural habitat. One adult and two juveniles of *trigonatus* were kept tethered in a brook 10 meters wide, for three weeks. They were tied by long ropes with a harness across the body at two points, so that they could move quite freely within an area of about 10 meters each. Each individual was placed beyond the reach of the others.

In the Apaporis basin *Paleosuchus* usually could be seen on the river banks much later in the evening than *Caiman sclerops.* The spectacled caimans appear between 7 and 8 P.M. and the smooth-fronted caimans between 9 and 10 P.M. In other places, for example, in the Río Inirida, *Paleosuchus* emerged as early as *Caiman.* Near the river beds the juveniles and occasionally larger specimens of

FIG. 38. Habitat of *Paleosuchus* in Colombia.

Paleosuchus commonly hide behind branches overhanging the river or beneath the quantities of fallen trees at the river's edge (the *palisadas*). In deep water the body is held at a somewhat greater angle with the surface than is that of the spectacled caimans. Whereas the latter always lie more or less directly beneath the surface, with their light-colored flanks visible, only the head and neck of *Paleosuchus* are to be seen. This makes *Paleosuchus* rather difficult to harpoon. In the water *palpebrosus* is easily recognized by its reddish brown cranial table, which is even more reddish in appearance when wet. *P. trigonatus*, when the characteristic snout is not visible, looks like a dark-colored *Caiman sclerops*. In the focus of the flashlight the eye-shine of both *trigonatus* and *palpebrosus* is always darker red than that of the species of *Caiman*. Only adults were observed on the river banks; some of them apparently had recently emerged from burrows beneath the water-level, for their heads and bodies were covered with wet clay. Many such openings were later observed during the main dry season when the water-level of the Río Pacoa was low. Natterer (1841) states that both *Paleosuchus* and *Caiman sclerops* inhabit such burrows.

In correlation with their habitat in swift water, the movements of both species of *Paleosuchus* are quick and agile. They are able to cross the river directly in the smaller rapids and even to swim against a strong current. When startled on the banks they jump suddenly into the water without gliding or running as the caimans do. Twice an adult *palpebrosus* jumped from a high sand bank over my dugout into the river, a distance of several meters. Such a leap seems to be accomplished by means of the hind limbs and tail. Harpooned specimens defend themselves much more vigorously than do the larger caimans, using both the jaws and the very flexible tail. A harpooned specimen jumped or climbed into my dugout several times. Once an adult *palpebrosus* found in a knee-deep narrow brook did not try to escape; it swam under water straight toward me, ready to attack. When harpooned, it jumped out of the water and bit the hunter accompanying me. On the other hand, when not cornered, the species of *Paleosuchus* seemed to be more shy than those of *Caiman*, even when not acquainted with human beings.

Smooth-fronted caimans were never to be observed in groups; they were always alone, even the juveniles. This seems to be associated with their very aggressive behavior toward one another. Such behavior was observed in several small juveniles in captivity, which hurt each other badly during the first night they were confined together. The adults seem to occupy a certain territory, as was observed in several cases in the Apaporis region and in the Llanos. In the Apaporis two specimens were observed for several weeks on the same rocks beside a small rapid, well protected by the current from being captured. In the upper Río Güejar (in the Llanos) one specimen was often seen resting on a fallen tree between rocks in a whirlpool. The "territory" may depend on the abundance of food in the rivers; in smaller brooks the specimens may have to wander more widely in search of prey. In several areas that were repeatedly investigated, new specimens of *Paleosuchus* were found after the original inhabitants had been captured.

Three *trigonatus* kept in captivity never came out by day, but they were very active at night after about 9 P.M. I observed several times how they captured smaller fishes, pushing the school toward the jaws by means of the tail and forming a circle with the entire body. During the day they rested on the bottom directly beside the bank, the juveniles in a depth of about 50 cm., among detritus, but not burrowed into the mud; the adult lay beyond a tree trunk at a depth of about 100 cm. The black longitudinal zone on the

head and the dense growth of algae on most of the body made these specimens extremely difficult to see. Every morning, following the direction of the rope, I thought that they had escaped during the night; even at a distance of less than one meter and in shallow water they were at first quite invisible. The black zone had a completely disruptive effect; the shape of the head seemed to be "dissolved" among the rotten leaves. This was also true for the body, covered by algae and also broken up by the black transverse bands. The adult specimen was easier to recognize on account of its size, but without the rope one never would have taken it for anything living —rather for some rotten tree branch covered densely by greenish algae. The single-crested part of the tail was the least camouflaged part of the animal. Although *palpebrosus* is more conspicuously colored, this species is likewise not without protective coloration in certain habitats.

In the Caño Cajuy in the Llanos, I waded in a small, shallow brook in search of *palpebrosus*. Wading against the current, in order not to disturb the specimens, I observed two adults on two different nights. They lay motionless on the bottom, which consisted of stones, gravel, and rotten leaves of different colors. At a distance of one or two meters, the reddish heads and the single-crested tails were visible, although somewhat indistinct among the leaves and stones. The outlines of the body were completely disrupted by the contrast of its color with that of the head. These specimens were respectively 1.40 and 1.42 meters in length. Apparently they had seen the approaching headlight but instead of escaping upstream they dived and remained motionless on the bottom.

Abundance.—In the Apaporis region *palpebrosus* was not rare, especially in the Río Pacoa where no Indians lived, and this species was obviously more abundant than *trigonatus*. If one knew their exact habitat, specimens could always be found. They appear to be less abundant than *Caiman sclerops*, partly because only one specimen is to be found within a given area. It must be emphasized, however, that six months of observations are insufficient to give an adequate report on abundance or scarcity. In the Llanos Orientales, on the other hand, *palpebrosus* seems to be really rare, or at least much more difficult to find. Only one of the experienced hunters, native of this area, knew vaguely that there is a "*cachirre negro*" in addition to the common *cachirre* (*Caiman sclerops*).

Enemies.—The only proven enemy in the Apaporis region is the Indian, who hunts smooth-fronted caimans for food but does not

eat the spectacled caiman. Dried skulls were several times found in Indian habitations. It may be that in regions permanently inhabited by Indians *Paleosuchus* becomes rare (as apparently in the Río Cananarí). The Indians, or most of them, distinguish the two kinds of *Paleosuchus* as animals good to eat; others from the Brazilian part of the Vaupés and Amazon had the same information.

Food.—Stomach contents of both species indicate a varied diet. In a specimen of only 94.2 cm. length (CNHM 69875) the stomach contained one snake 50 cm. long (red and white, probably a coral snake); one fish; one fresh-water shrimp; two large aquatic beetles; and fifteen small stones. Aquatic spiders, fresh-water shrimps, crabs, fishes, and beetles were noted in other stomachs. In adults the remains of small rodents and of small crocodilians (perhaps juveniles of the same species) were found, but fishes up to a length of 30 cm. were apparently the principal food. Considerable quantities of small pebbles were always found, up to 69 in one adult (CNHM 69867). Even very small juveniles swallow small stones, as shown by x-ray photographs of a specimen of *palpebrosus*, 25.7 cm. in length (MVZ 2016). One juvenile *trigonatus* 28.3 cm. long (CNHM 63888) had no stones in its stomach. Parasitic nematodes were occasionally found in the stomach.

Size.—Boulenger (1889) gives a length of 1.20 meters for *palpebrosus*, and 1.40 meters for *trigonatus*. The largest *palpebrosus* recorded in the literature is a specimen measuring 1.72 meters (Lueder-waldt, 1926) from Ituverava, Brazil. For Colombia, the largest *palpebrosus* (♂ CNHM 69871) collected was 1.545 meters in length, and the largest female (CNHM 69868) measured 1.23 meters. The largest *trigonatus* male (CNHM 81980) measured 2.256 meters, and the largest female (Medem no. 15) 1.33 meters. The average length of a full-grown specimen is about 1.3 meters. At that size their skulls indicate that they are old individuals, some of them showing deterioration of the bone.

Reproduction.—No personal observations were made on breeding habits, hatching period, or nest-building habits, and I find no data in the literature on the eggs and embryonic development. According to reports of experienced hunters, the egg-laying period in the Vaupés territory probably is the dry season (December–March) and mainly in February or March. On the other hand, reports from experienced hunters in the Río Apaporis say that *Paleosuchus* never lays its eggs in the dry season. The females wander upstream to the smallest brooks to make their nests beside the bank or not far from

the water in the woods. For this purpose they gather decayed plants by means of the tail into a mound of about 80 to 100 cm. in breadth and 80 cm. in height. This is quite like the nest-building of *Caiman sclerops*. The hatchlings appear in April or May. From the Llanos Orientales I have the following report: In mid-December, 1949, a nest was found near the Río Guatiquía (vicinity of Villavicencio). It was situated beside a small brook in a very dense piece of woods. The female, apparently guarding the nest, attacked the approaching hunter and was killed. The nest, consisting of piled-up, rotten leaves, contained about 18 eggs. Señor Castro Losada, who gave me this information, emphasized that the female was a *"cachirre negro"* (*P. palpebrosus*), not a common *cachirre* (*Caiman sclerops*). Señor Alirio Mejia informs me that he discovered a nest of *palpebrosus* in November, 1956, beside a small stream in the lower Apaporis area. The 22 eggs, obviously recently laid, as they were not yet stained by decomposing leaves, were as long as eggs of *Caiman sclerops* but smaller in diameter. The female escaped into the water. Two small *P. palpebrosus* captured December 1, 1950, in a small brook near the Río Güejar (in the Llanos Orientales) were apparently not older than one or two months.

It seems likely that the mating and egg-laying period extends through most of the year, with the exception of the principal rainy season (April to July) when nests could not be made in the flooded areas.

Adaptation.—Kälin (1933) came to the conclusion that the specific characters of *Paleosuchus* are based on its tendency to a terrestrial mode of life. Although there is certainly specialization, it can scarcely be described as an adaptation to terrestrial habits. As found in the field, *Paleosuchus* obviously has no greater trend to such habits than the other caimans, the smooth-fronted caimans being in fact more aquatic. In the rain forests the streams do not dry out in the dry season; and if they do—as in the Llanos—*Paleosuchus* migrates to the rivers or aestivates, as *Caiman sclerops* does (Natterer, 1841).

Paleosuchus obviously represents a crocodilian well adapted to life in swift-running waters. The extreme ossification of the head in adults, including the completely ossified palpebrals, and the strong dermal armor, mainly that of the neck, seem to form an effective protection against the rocks in swift waters. The very pointed teeth, more curved toward the rear, are adapted for grasping elusive prey in turbulent waters. Speed and quickness characterize both species. The differences in habits between *palpebrosus* and *trigonatus* are still

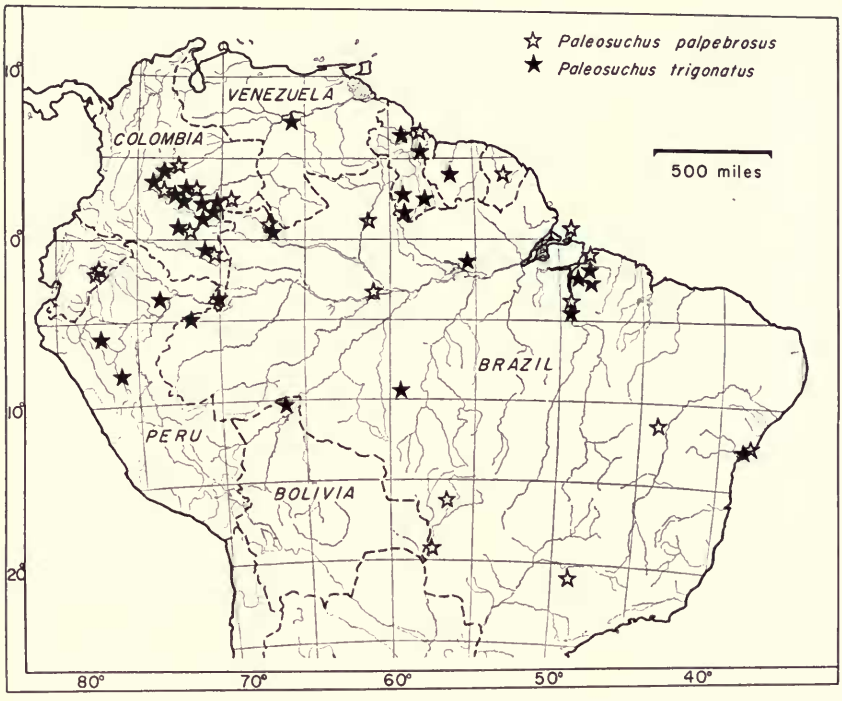

FIG. 39. Localities of specimens examined and of reliable records in the literature.

scarcely understood. The growth of algae on *trigonatus* only indicates that the specific ecological niches are a little different, *trigonatus* living in less turbulent and therefore also warmer waters than *palpebrosus*. *Caiman sclerops*, which lives in quiet water, never appears to develop a growth of algae.

DISTRIBUTION

Paleosuchus palpebrosus.—The southernmost locality of *palpebrosus* is Ituverava, São Paulo, Brazil; thence the border of the range extends westward to Corumbá, Mato Grosso, and Villa Maria on the upper Río Paraguay, and to the Río Pastaza in Ecuador. The northernmost localities are the Sabana de San Juan de Arama, Meta, and the environs of Villavicencio, Colombia, situated on the edge of the Cordillera Oriental at an altitude of 400 meters. Eastward the range includes British Guiana, Surinam, and Cayenne. The species is found on the Island of Mexiana at the mouth of the Amazon. Although the locality, Bahia, given by Spix (1825) and by Spix and

Martius (1828) has always been questioned, their first-hand accounts leave no doubt that *palpebrosus* once occurred there.

Paleosuchus trigonatus.—The southernmost locality for *trigonatus* appears to be Bahia; to the west it is known from the Río Abuna, Bolivia, and from the Huallaga and Ucayali in Peru. At the north, it is known from the Ríos Sansa and Ocoa, Colombia, and as far north as Angostura (Ciudad Bolivar) on the Río Orinoco, Venezuela. To the east, it is found mainly in British Guiana, Surinam, and Mexiana Island.

Both species apparently occur together not only over most of the Amazon and Orinoco basins, but even as far as extreme eastern Brazil (fig. 39). In general, both species are closely associated with the South American rain forest, and the genus must be thought of as having evolved there. The broad overlap of the ranges of the two species appears to fall under the general statement of Allee, *et al* (1949): "Tropical areas often contain both more isolating factors and more ecological niches, and these together constitute a more satisfactory explanation of the greater diversity of the species than increased mutation caused by warmer temperatures. . . ."

SUMMARY

Thirty-four specimens of *Paleosuchus palpebrosus* and fifty *P. trigonatus* were examined, including specimens from widely separated localities, but mainly from Colombia.

It is demonstrated that, of the two species, *P. trigonatus* is the more generalized form; this is true not only for its skull characters, but for its scalation. *P. trigonatus* shows all steps of development, from the apparently more primitive *trigonatus* scale arrangement to the more "advanced" one, which is specific for *P. palpebrosus*. *P. palpebrosus* is the more specialized, even though certain "*trigonatus*" characters occur in juveniles, and therefore it may be considered as derived from the former species.

There is a great difference in coloration between the two species in both adults and juveniles. The color pattern has a cryptic effect, evident when one observes these animals in the field.

Both species have the same preferred habitat, swift or turbulent waters in the tropical rain forests. The extremely developed ossification of the skull, the very strong dermal armor, and certain features of behavior I interpret as adaptations to this special habitat.

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